DESCRIPTION OF AN UPPER MIOCENE ALBATROSS FROM BEAUMARIS, VICTORIA, AUSTRALIA, AND A REVIEW OF FOSSIL DIOMEDEIDAE

By H. E. WILKINSON

Assistant Curator of Fossils

Abstract

An incomplete bill of an albatross from Upper Miocene marine sands at Beaumaris, Victoria, is shown to belong to the genus *Diomedea*, and to be distinct from all previously described species of that genus. It is described as *Diomedea thyridata* sp. nov., and its relationships with living and fossil albatrosses are discussed. The fossil record of the family Diomedeidae is reviewed, and the significance of this fossil for an understanding of the evolution of the family is demonstrated.

Introduction

The palaeontological collection of the late Dr G. B. Pritchard was purchased by the National Museum of Victoria in 1950. It included a large number of vertebrate fossils from Upper Miocene marine beds at Beaumaris, on the E. shore of Port Phillip Bay, Victoria. Most of these came from the nodule bed at the base of the Black Rock Sandstone. However, there were a few which had apparently been collected in situ from above the nodule bed, as judged by the nature of the matrix still adhering to them, and among these was the fossil described in this paper. There is no reason to doubt that the fossil was collected by Dr Pritchard from Beaumaris, but there was no information with it apart from the locality, so its exact provenance is not known. When the fossil was prepared a sample of matrix was retained, part of which was sent to Mr A. C. Collins (Honorary Micropalaeontologist) for examination. His report (dated 25.2.1967) was: 'The washed material consisted mostly of small angular quartz grains iron-stained and tending to aggregate in granules which did not break down in dilute HCl. There was some calcareous material but not a large proportion, rare glauconitic grains, and very few forams, poorly preserved and scarcely identifiable, mostly *Elphidium* sp. There is no positive evidence of age. The material is similar in lithology to other Beaumaris material in my possession, but differs in lacking the microfossil fauna. It could be from a leached horizon.'

The foraminiferal evidence is inconclusive, but there are other reasons for believing that this fossil came from the Black Rock Sandstone above the nodule bed, and these are listed below.

1. It is not likely that the bill could have survived the conditions under which the nodule bed formed. Fossils from the nodule bed are typically highly mineralized, well worn and often highly polished, whereas the albatross bill is relatively lightly mineralized, and although damaged before burial, is on the whole well preserved.
2. Scattered vertebrate remains with similar preservation and matrix are found above the nodule bed.
3. The oxidized matrix and absence of carbonate cementation support this interpretation.

The latest description of the section at Beaumaris, which includes a summary of earlier work, was given by Kenley in 1967. The sequence of marine rocks forming the lower part of the cliffs, including the nodule bed, is the type section for the Cheltenhamian stage (Singleton 1941) which is probably of late Upper Miocene age. Stirton, Woodburne and Plane (1967) place their 'Beaumaris Fauna' in the Lower Pliocene, mainly on the basis of the stage of evolution of the Diproto-dontid *Zygomaturus gilli* Stirton 1967, but this evidence is not as strong as that for a Miocene age. T. A. Darragh (pers. comm.) says: 'the Miocene age is based on the occurrence of the pelagic cephalopod *Aturia* which is restricted to the Eocene, Oligocene and Miocene in other parts of the world. This genus is absent from the younger Kalimnan stage which has been traditionally correlated with the Lower Pliocene.' It is reasonably certain then that the fossil came from the lower part of the cliffs at Beaumaris, and is therefore of Upper Miocene age.

This is the first record of the family Diomedeidae from the Tertiary of Australia, but this is not surprising since albatrosses are extremely rare as fossils. The fossil record of the family is reviewed in this paper, but it can be noted here that previously recorded occurrences are based on isolated post-cranial elements, so direct comparison between them is usually not possible. Previous records of fossil birds in Australian Tertiary marine rocks have been confined to the order Sphenisciformes (penguins), and Simpson (1965) summarized their occurrence.

Acknowledgements

Systematic Description

Order PROCELLARIIFORMES Fürbringer 1888

Family DIOMEDEIDAE (Gray) 1840

Genus **Diomedea** Linnaeus 1758

Diomedea thyridata sp. nov.

Pl. 3, fig. 1; Pl. 4, figs. 2, 5.

ETYMOLOGY: Gr. *thyris, -idos* f. dim., window or small door, in allusion to the relatively small inner posterior aperture of the Antrum of Highmore.

MATERIAL: Holotype, N.M.V. P24172, G. B. Pritchard Coll.

TYPE LOCALITY: Beaumaris, Victoria, almost certainly from above the nodule bed in the Black Rock Sandstone.

AGE: Uppermost Miocene (Cheltenhamian).

DIAGNOSIS: A *Diomedea* comparable in size to the smaller living species, with a bill of the '*melanophris* group' type, distinguished from all other species by the following combination of characters: a high-crowned rounded culmenal ridge, relatively large narial apertures, a bony floor to the apertures, nasal bone behind the apertures with nearly vertical posterior border, and a width of about 10 mm, inner posterior aperture of the Antrum of Highmore wider than high and relatively small, dorsal outline of bill fairly strongly concave, nasal sulci more or less median in position, slight expansion of the nasal processes of the premaxilla behind the narial apertures.

DESCRIPTION: The fossil consists of the proximal two-thirds of the upper bill of an albatross. The strongly hooked anterior portion (the unguis) is entirely lacking, but the morphology of the preserved portion is so typical of the family that there can be no reasonable doubt that the fossil bill bore such a hook in life. The terminology used is that of Pycraft 1899, except for the addition of the term 'culmenal ridge' for the structure formed by the fusion of the nasal processes of the premaxilla.

Total length of the fossil is 68·5 mm, and comparison with living species suggests that the length of the bill in life was between 100 and 105 mm. It has a maximum width posteriorly of 19·5 mm, and when allowance is made for abrasion, this gives an estimated width in life of 22 mm. At the same level, the fossil has a maximum height of 26·2 mm. There is little evidence of any distortion during fossilization, so these dimensions are probably meaningful. The culmenal ridge is transversely rounded, and because of the near median position of the nasal sulci, is a very prominent feature of the fossil bill. It is 8·1 mm wide just anterior to the narial apertures, at which level the bill has a width of 15·8 mm. The culmenal ridge consists of the fused nasal processes of the premaxilla, and behind the narial apertures, the sutures between these and the nasal bones are just detectable on the fossil. The maximum width of the nasal processes in this area is 8·5 mm, i.e. there is a slight expansion of the nasal processes behind the narial apertures.

When viewed laterally, (Pl. 3, fig. 2) the dorsal profile is quite strongly concave and is roughly paralleled by both the nasal sulcus and ventral profile. The nasal sulcus, which lies at the contact of the nasal and maxillary processes of the premaxilla, is 2·5 mm wide, and rather wider and deeper than in related living albatrosses. The maxillary processes of the pre-maxilla are strongly-built plates, sloping steeply downwards and outwards. The sharp flanges on the ventral edges of these processes in living albatrosses are absent in the fossil, but this is certainly due to abrasion before burial. The holorhinal narial apertures lie between the processes of the premaxilla, and are bounded posteriorly by the nasal bones. They are approximately 19 mm long and have a maximum height of about 6 mm. The maxillary processes bend inwards below the apertures to form a shelf of bone which merges imperceptibly into the nasal sulcus anteriorly. This bone shelf is at least 3-4 mm wide. The depth of maxillary process below it, in the middle of the aperture, is 9·4 mm, to which can be added 1·0-1·5 mm for the missing flange at its ventral border. The flange has broken away along a line of weakness visible on the bills of living albatrosses. The measurement from the same position to the centre of the culmenal ridge is 10·3 mm. Thus the base of the narial aperture is very nearly in the midline of the bill. The minimum width of nasal bone behind the narial apertures is 10 mm, its posterior border in this area being very nearly vertical. The nasals extend onto the dorsal surface of the bill, and contact the nasal processes of the premaxilla behind the narial apertures.

D

Ventrally, (Pl. 2, fig. 2) the fossil has the deep palate and slit-like premaxillary vacuity typical of the family. The latter is almost complete and is estimated to have been 41 mm in length, with a width of 2.5 mm. The vacuity separates the ventral portions of the maxillary processes of the premaxilla, but in the anterior portion of the palate these fuse to form a bony palatal roof in living albatrosses. This anterior region is only just represented on the fossil. In the vicinity of the anterior end of the premaxillary vacuity, the ventral border of the maxillary processes forms the apex of a triangular area which widens posteriorly, and faces outwards and downwards. Although considerably abraded, this area is recognizable on the fossil, and its apex could make a reference point for a rough comparison of palate widths. In the fossil the internal palate width at this point is 8.0 mm, the bill being 12.5 mm wide.

The maxillo-palatines in albatrosses are concavo-convex lamellae which are extensively fenestrated. On the palate they appear as a pair of thin processes lying between the palatines, and pointing posteriorly. This region is represented on the fossil, although it has suffered some abrasion, and in fact most of the adjacent palatine bones have been removed by erosion, allowing a view of the inner portion of the maxillo-palatine. The hollowed-out chamber which lies within the somewhat scroll-like maxillo-palatines is the Antrum of Highmore. In living albatrosses, there are generally three posterior apertures of this chamber; two lie vertically above each other close to the outer surface, while the third (normally the largest) lies internally to them. These apertures are taxonomically significant, and it is fortunate that they are partly preserved in the fossil. The inner aperture is larger, wider than it is high, and relatively small compared to those of its living relatives. The palatines are barely represented on the fossil, and give no information of diagnostic value. The ventral tip of the vomer is useful in distinguishing albatross species, but is not preserved on the fossil.

Discussion

The osteology of birds is a subject which has been relatively neglected this century when compared with the study of other vertebrate groups, and especially when compared with the voluminous literature on most other aspects of ornithology. The albatrosses have been no exception. The two principal osteological descriptions are those of Forbes (1882) and Pycraft (1899), but both are comparative descriptions of the family as a whole in relation to other Procellariiforme birds. There has apparently been no study of the osteology of the family Diomedeidae at the species level, and this has been a considerable handicap in the preparation of this paper. I have had access to skulls of the seven species which include the Australian coastline within their wintering ranges but the non-Australian species present a problem because illustrations of the living birds have the various horny plates of the ramphotheca in place, and illustrations of the skulls are not available. Very little can be deduced about their osteology, apart from gross morphology, which of course bears some relationship to the arrangement of the plates. Coues (1866) pointed out that the bills of albatrosses are diagnostic at the specific level, and described those of several species. However, his work is of limited value for the present purpose, because it is concerned with the appearance of the bill in life, and contains little information on osteology. The following discussion is therefore based mainly on comparisons with the Australian albatrosses.

1. Generic Identity of the Fossil

Two genera of living albatrosses are recognized at the present time, namely

Table of measurements — specimen columns, measurement rows.

Measurement	Phoebetria fusca W 6328 Portland, V.	Phoebetria palpebrata W 6329 Portland, V.	Diomedea exulans W 6322 Portland, V.	Diomedea cauta B 705 Mewstone Rock, Tas.	B 4445 Portland, V.	Diomedea chlororynchos B 704 Queenscliff, V.	B 4122 Brighton, S. Aust.	B 4746 Waratah Bay, V.	Diomedea thyridata sp. nov. P 24172 U Miocene Beaumaris, Vic.	Diomedea melanophris W 2673 Portland, V.	B 9678 Portland, V.	B 2455 Heard Island	B4530 Portland	Diomedea chrysostoma B 6368 Portland, V.	B 6771 " "	B6826 " "	W 6326 " "
1. Length of bill	98	95	150	113	113	100	110	114	est. 105	102	98	103	99	104	96	97	98
2. Max. width at base of bill	21.3	20.5	40.5	28.4	30.2	24.5	23.7	24.2	est. 22	24.6	25.7	27.6	24.8	24.2	22.4	23.7	26.6
3. " " height " " " "	29.7	26.2	38.3	33.5	34.1	28.1	27.2	28.9	26.2	29.0	28.5	31.3	30.8	30.5	28.5	29.2	30.2
4. Width of culmenal ridge just anterior of narial apertures	10.0	9.7	17.4	11.5	10.2	7.4	8.1	7.8	8.1	8.7	8.6	10.0	9.2	8.8	7.4	7.8	9.0
5. Width of bill at same level	15.4	14.9	30.1	20.5	22.1	16.4	18.6	18.1	15.8	17.4	17.8	19.1	17.5	12.7	15.3	17.9	19.4
6. 4 as % of 5	65.0%	65.5%	58.0%	57.5%	46.0%	45.0%	43.5%	43.5%	51.5%	50.0%	48.0%	52.5%	52.5%	69.0%	48.5%	43.5%	47.0%
7. Max. width of nasal processes of premaxilla behind narial apertures	7.7	7.0	12.5	10.8	8.6	7.3	7.1	7.9	8.5	8.9	9.1	11.5	10.4	8.0	7.7	8.8	8.4
8. Depth of outer border of maxillary processes of premaxilla below narial apertures	6.4	6.1	13.3	15.5	15.2	12.3	11.5	12.0	est. 10.5	10.5	11.9	11.0	11.2	12.0	10.5	10.8	11.9
9. Height of bill at same level	19.3	18.6	31.6	26.8	24.9	22.9	19.4	20.8	–	22.4	23.7	23.7	22.7	22.3	21.3	21.1	23.4
10. Minimum width of nasal bone behind narial apertures	c. 8	5.4	c. 6	12.0	16.4	10.9	11.4	11.0	10.0	6.5	6.8	11.7	8.7	11.0	6.5	7.0	10.1
11. Approx. dimensions of) Length / narial apertures) Height	15.0 / 6.0	19.0 / 6.5	27.0 / 7.5	17.0 / 7.0	15.5 / 5.0	11.5 / 4.0	15.0 / 4.0	13.5 / 4.0	19.0 / 6.0	22.0 / 7.5	20.0 / 7.5	16.0 / 7.5	15.0 / 6.5	15.5 / 7.0	21.0 / 7.0	19.0 / 6.5	16.0 / 6.0
12. Length of premaxillary vacuity	39.5	32.0	47.0	42.0	43.0	42.8	51.0	47.0	41.0	47.0	37.0	46.0	40.0	40.0	39.0	42.0	39.0
13. 12 as % of 1 (bill length)	40.3%	33.5%	31.3%	37.0%	38.0%	42.6%	46.4%	45.2%	40.1%	46.0%	37.7%	44.7%	40.3%	37.5%	40.7%	43.3%	39.5%

TABLE 1

Table of measurements from a series of bills of the Diomedeidae which includes the Australian coast within their ranges. The characters used can either be directly measured on the fossil or estimated with a reasonable degree of accuracy. Only one or two representative examples have been measured of those species which have no close relationship with the fossil, but all available material of its modern relatives has been measured. All measurements in mm.

Diomedea and *Phoebetria*, (Peters 1931, pp. 41-46). Other genera have been proposed from time to time for various species of *Diomedea*, but the instability of their nomenclature is in marked contrast to the stability of *Phoebetria*. This is not surprising, because the similarities between the species of *Diomedea* are greater than their differences, while *Phoebetria* is clearly distinct. Although grouping of the species of *Diomedea* on bill characteristics is possible (see below), it is doubtful whether the use of even subgeneric names is warranted. *Phoebetria* contains two species, *P. fusca* (Hilsenberg) and *P. palpebrata* (Forster), which have in common many features which set them apart from *Diomedea*. Murphy (1936) pointed out that *Phoebetria* is distinguished by the dark plumage of adults, much larger tail, cuneate form, and the persistence of a 'primitive' character in the bill, namely a sulcus dividing the plates of the lower mandible. Before attempting to establish the generic identity of the fossil, it was necessary to ascertain whether the generic distinction between *Diomedea* and *Phoebetria* could be supported on characters of the upper bill alone. It was found that *P. fusca* and *P. palpebrata* have in common morphological features of the upper bill which clearly separate them from *Diomedea* spp. The most important of these are listed in Table 2.

TABLE 2

Osteological characters of the bill which can be used to separate the genera Diomedea *and* Phoebetria

Character	Diomedea	Phoebetria
Inner posterior aperture of Antrum of Highmore	Always present; larger than two outer apertures	Usually obsolete; if present, very small
Depth of outer border of maxillary process of pre-maxilla below middle of narial aperture	>10 mm.	<7 mm.
Width of culmenal ridge as % bill width just anterior of narial apertures	43-57%	c. 65% (i.e. relatively broad)
Nature of palate	Not as deep as in *Phoebetria* relative to palate width	Much deeper than in *Diomedea* relative to palate width

Comparison of the data in Table 1 with Table 2 clearly shows that *D. thyridata* sp. nov. differs from species of *Phoebetria* in the same features as species of *Diomedea* do, and has no close affinity with the former. On the other hand, there is no character on the fossil which cannot be at least approximately matched in some species of *Diomedea*. Its specific distinctness is based on a unique combination of characters within that genus. Furthermore the fossil belongs to one of the two main groups within *Diomedea*, as will be shown below. Clearly there could be no possible justification for the erection of a new genus.

2. Comparison with living species

The two species of *Phoebetria* are excluded from further discussion, because they can be separated from the fossil on generic characters, as shown above. Coues (1866) rejected the splitting of *Diomedea* s. l. prevalent in his time (and maintained by many other workers until well into this century), but introduced the concept of 'groups' of albatrosses based on bill characters, which I have followed

in preference to formally re-introducing the appropriate generic names as sub-genera. This must await a really detailed study of the family as a whole, but the groupings on bill characters do seem to indicate something of the relationship within the genus *Diomedea*.

(a) *D. melanophris* group

This group includes the majority of the smaller albatrosses, and is virtually confined to the S. Hemisphere at present. Two sub-groupings are possible, but these are not sharply differentiated, and the fossil shows affinities with both. More specifically it shows relationships both to *D. melanophris* Temminck (Pl. 3, fig. 3; Pl. 4, figs. 3, 6) the 'typical' member of one sub-group, and to *D. chlorohynchos* Gmelin (Pl. 3, fig. 1; Pl. 4, figs. 1, 3) which belongs to the other. The *melanophris* sub-group includes *D. chrysostoma* Forster and *D. irrorata* Salvin, and is characterized by a prominent, high-crowned culmenal ridge, large narial apertures and relatively narrow maxillary processes. The placing of *D. irrorata* here is tentative, but in describing it Salvin (1883) said 'It appears to come next to *D. melanophris* having the bill similarly constructed . . . . but the bill is much larger'. Illustrations of the living bird certainly support such an affinity, but little else can be said about it here. *D. chrysostoma* has a lower crowned culmenal ridge than either *D. melano-phris* or *D. thyridata* sp. nov., and partly bridges the gap to the *chlorohynchos* sub-group, which is characterized by expansion of the maxillary processes of the premaxilla with correspondingly low-crowned culmenal ridges. Affinities with *D. thyridata* sp. nov. are shown by the presence of a bony floor to the small narial apertures, and a relatively wide expanse of nasal bone behind them. Included in this sub-group is *D. bulleri* Rothschild, of which I have seen neither specimens nor a good illustration, but it is apparently closely related to *D. chlorohynchos* and certainly seems to have a similar bill structure. *D. cauta* Gould belongs here also, but its larger size and more robust nature of its bill distinguish it from its smaller relatives.

Basically, *D. thyridata* sp. nov. is most closely related to *D. melanophris*. Apart from the features mentioned above, it shares with that species a characteristic slight expansion of the nasal processes of the premaxilla posterior to the narial aper-tures, and a premaxillary vacuity of similar length. This in turn suggests a bill of similar length, because the vacuity in *D. chlorohynchos* is several millimetres long-er, due to the more elongate bill. It is not unlikely that *D. thyridata* sp. nov. repre-sented the ancestral form which gave rise to *D. melanophris* and that the affinities with *D. chlorohynchos* place it close to being the common ancestor of both. Cer-tainly it indicates that the '*melanophris* group' as a whole has a history dating back at least to the Upper Miocene.

(b) *D. exulans* group

This includes the two largest living species, *D. exulans* Linné and *D. epomo-phora* Lesson, and *D. albatrus* Pallas. Coues (1866) also included *D. nigripes* Audubon, but this species is somewhat atypical in certain respects. The bill of *D. exulans* is readily distinguished from the fossil by its much greater size and more robust character, coupled with distinctive morphological differences, which include broad low-crowned culmental ridge, deep but wide palate, and more out-ward sloping maxillary processes of premaxilla. It is the only species of this group of which I have seen specimens, but illustrations of the other species show that *D. thyridata* sp. nov. has no close affinity with this group. *D. epomophora* is

closely related to *D. exulans*, but has a bill which is even broader than that of
D. exulans (Murphy 1936). *D. albatrus* has a bill of the 'same fundamental char-
acters' as *exulans*, according to Coues, but differs in having a much less concave
dorsal outline. In fact, it is almost straight to the midpoint, where it flattens, and
hardly rises to the unguis. *D. thyridata* sp. nov. has a smooth continuous curve in
a fairly concave outline. *D. nigripes* has a bill which is relatively short, with an
almost straight dorsal outline, reminiscent of *Phoebetria*. The dark plumage is
another character shared with that genus, as is the relatively short bill, with
narrower maxillary processes than in typical *Diomedea*, but the depth and robust
form of the bill in *nigripes* apparently ally it to the *D. exulans* group. Figures of the
bills of *D. nigripes* and *D. albatrus* given in Seebohm (1890, pp. 260-3) show these
characters. *D. immutabilis* may belong to this group also, because in his descrip-
tion of the species Rothschild (1893) says 'This albatross belongs to the typical
section of *Diomedea* as limited by Mr Salvin', and the 'typical group' was based on
D. exulans, type species of the genus. Thus it can be seen that *D. thyridata* sp. nov.
has no close relationship with this group, whereas it is clearly of '*melanophris*
group' type, as shown above.

3. Comparison with fossil Diomedeidae

The fossil record of the family is very meagre indeed. There are two Lower
Tertiary fossil birds which Brodkorb (1963) doubtfully referred to the Diomedei-
dae. The oldest of these is *Gigantornis eaglesomei* Andrews (1916) based on an
incomplete sternum from the Middle Eocene Ameki Formation of the Omobialla
District of S. Nigeria. The bird it belonged to was thought by Andrews to have
been about twice the size of *D. exulans*. There is no certainty that *Gigantornis* was
an albatross, and even if it were it is most unlikely that it had any close relation-
ship with the genus *Diomedea*.

The other Lower Tertiary species is *Manu antiquus* Marples (1946) which was
based on an incomplete furcula from the Upper Oligocene (Duntroonian) Maera-
whenua Greensand from near Duntroon, N. Otago, S. Island of New Zealand. It is
much more likely that this was a true albatross, as its furcula was comparable to
that of *D. exulans* in some respects, being fairly close in size, though the latter 'has
a slightly greater angle between the rami'. Marples concluded that the specimen
differed generically from *Diomedea*, so whether a true albatross or not, it obviously
bore no close relationship to *D. thyridata* sp. nov. Marples also recorded shaft
fragments of an ulna and radius from the same deposit 'which might have belonged
to the same or a slightly smaller species'.

There are two records of Miocene albatrosses from N. America. The first was
recorded by Loye Miller in 1935 from the Upper Middle Miocene Temblor Forma-
tion at Lomita, California, U.S.A. An impression of 'the wrist and proximal bones
of the hand' was referred to the Diomedeidae by Miller on the characters of the
carpometacarpus and of the pollex. The specimen was 'slightly smaller than *D.
nigripes* and slightly greater than *D. immutabilis*'. This would seem to suggest that
the albatross from Lomita was smaller than the other N. American Miocene
species, *D. californica*, which Miller described in 1962. This species was based on
a distal portion of a left tarsometatarsus from the Temblor Formation at Shark-
tooth Hill, Kern County California. Unfortunately, comparisons were limited to
D. albatrus, *D. exulans* and the English Pleistocene species *D. anglica* Lyddeker
(1891a). He showed that the tarso-metatarsus of *D. anglica* was slightly larger
than that of *D. albatrus*, although the width across the trochleae was the same in

both. That of *D. californica* was larger and stouter than either, and very much shorter than that of *D. exulans*. Comparisons of his figure with tarso-metatarsi of the albatross species available to me, but not considered by Miller, indicate that only that of *D. cauta* approaches the fossil in size and proportions. However, there is no close resemblance, since the trochleae are relatively shorter in *D. cauta*, and the shaft is narrower. The length of the bone is only about two thirds of that of Lyddeker's figure of *D. anglica*, so clearly *D. cauta* has no close affinity with *D. californica* or *D. albatrus*. On the other hand, comparison with the tarsometatarsus of *Macronectes giganteus* (Giant Petrel) revealed a striking similarity in appearance and proportions, and in particular in the morphology of the shaft and length of the trochleae. The principal difference is the greater width of the inner trochlea of the fossil, which is one of the features on which Miller separated the fossil from *D. albatrus*. This casts some doubt on the generic and family assignment of *D. californica*, although it should be pointed out that *Macronectes* is virtually confined to the S. Hemisphere at the present time. The giant petrels have large, strongly built bills somewhat reminiscent of those of albatrosses, but have united nostrils on the top of the bill like all members of the order Procellariiformes, other than the family *Diomedeidae*.

D. *thyridata* sp. nov. has lateral, separate nostrils, showing that this feature was present as far back as the Late Miocene at least. Even if the re-examination of the type of *D. californica* showed it to be a true *Diomedea*, the similarities to *Macronectes* are certainly interesting, and require some explanation. It is not likely that *californica* bore any close relationship to *D. thyridata* sp. nov. especially if its affinities do lie with *D. albatrus*, as Miller suggested.

There are two records of Pliocene albatross fossils, one from N. America, and one from England. The former is from the Lower Pliocene Bone Valley Formation of Pierce, Polk County, Florida, U.S.A., and was recorded by Wetmore (1943) as *D. anglica*, although this was regarded as doubtful by Brodkorb in his catalogue of 1963. The English specimen is from the Upper Pliocene Coralline Crag of Foxhall, Suffolk, England, and consists of an ulna of albatross type, tentatively referred to *D. anglica* by Lyddeker (1891b). It cannot be directly compared to the type of that species and its identity is therefore unknown.

Diomedea anglica Lyddeker (1891a) was based on a right tarsometatarsal and associated proximal phalanx of digit *iv* from the Lower Pleistocene Red Crag of Foxhall, Suffolk, and was said by its author to be intermediate in size between *D. exulans* and the smaller living species. Miller (1962) has pointed out that the tarsometatarsus is like that of *D. albatrus*, although relatively more elongated. The tarsometatarsi of *D. cauta* and *Macronectes giganteus* were compared to Lyddeker's figure of *D. anglica*, but the former is a shorter, relatively stouter bone, while the latter is more like it in proportions, but is a little shorter, and differs in morphological details. It would appear that *D. anglica* is a true *Diomedea*, and probably directly ancestral to the living *D. albatrus*, or perhaps could even be conspecific, if a sufficient range of specimens were examined. In any case, there is no obvious relationship with *D. thyridata* sp. nov.

Late Pleistocene-Early Holocene albatross fossils are presumably all of living species, and are not of any importance for this discussion.

4. Significance of *D. thyridata* sp. nov.

This is the first record of a fossil *Diomedea* from the S. Hemisphere, and the oldest undoubted record of the genus, if the *Macronectes* affinities of the slightly

older *D. californica* are sustained. *D. thyridata* sp. nov. shows that the '*melanophris* group' of *Diomedea* had evolved by the Upper Miocene, and that this predominantly Antarctic-Subantarctic group was present in the S. Hemisphere then. The '*exulans* group' has a N. Hemisphere fossil record going back to the Miocene also, if *D. californica* is a true *Diomedea*. The affinity with *Macronectes* of this fossil, and that of *D. nigripes* with the more 'primitive' *Phoebetria*, suggest that the '*exulans* group' is closer to the ancestry of albatrosses, and that the '*melanophris* group' may have evolved from it. This is highly speculative, and would need a much better fossil record for proof. It is clear that the separation of the two groups extends well back in time. Furthermore, as suggested above, *D. thyridata* sp. nov. is probably ancestral to the sub-groups within the '*melanophris* group' itself.

The partial bill from Beaumaris is also the first record of cranial material of a Tertiary albatross. It shows that the albatrosses were already essentially modern in appearance, if bill structure is any guide to this. Lateral nostrils and prominent nasal sulci demonstrate that the physiologic mechanisms for salt elimination were probably similar to those of living albatrosses. The nasal glands lie above the orbits, and their secretions pass through the nostrils and along the sulei to drip off the end of the bill. It is certain that the origins of this mechanism lie much further back in time than the late Miocene.

Finally, it can be noted that the Black-browed Albatross is a comparatively frequent visitor to Port Phillip Bay at the present time, in contrast to its more purely oceanic relatives, and the presence of remains of its Miocene ancestor at Beaumaris is therefore quite understandable. This is analagous to the situation in California where Miller (1962) noted that *D. albatrus* was much more frequently seen near shore than *D. nigripes*, and it is therefore not surprising that *D. californica* shows closer affinities to the former. It is much more likely that an albatross of habits similar to *D. melanophris* would come close enough to shore to be incorporated in shallow water sediments like those at Beaumaris.

The shoreline was not more than a few miles E., and faunal evidence suggests at least a partially enclosed bay (T. A. Darragh pers. comm.). *D. chlororhynchos* is rarely seen in Victorian waters, but is commoner further W. towards the Indian Ocean (K. G. Simpson pers. comm.). If *D. thyridata* was really ancestral to both, then obviously some kind of geographical separation would have been necessary for speciation to occur. In this connection, it is of interest to note that the breeding ranges of *D. melanophris* and *D. chlororhynchos* are mutually exclusive at the present time.

References

ANDREWS, C. W., 1916. Note on the sternum of a large carinate bird from the (?) Eocene of Southern Nigeria. *Proc. zool. Soc. Lond.* for 1916, pp. 519-524.

BROKDORB, P., 1963. Catalogue of fossil birds, Pt. I. *Bull. Fla. St. Mus.* 7(4): 241-2.

COUES, E., 1866. Critical review of the family Procellariidae Pt. V embracing the Diomedeinae and the Halodriminae with a general supplement. *Proc. Acad. nat. Sci. Philad.* 18: 172-188.

FORBES, W. A., 1882. Report on the anatomy of the petrels. *H.M.S. "Challenger" Report.* 4(11): 41.

KENLEY, P. R., 1967. Chapter 'Tertiary' in The Geology of Melbourne. *Bull. geol. Surv. Vict.* 59: 30-46.

LYDDEKER, R., 1886. Note on some Vertebrata from the Red Crag. *Q. Jl. geol. Soc. Lond.* 42: 366-367.

————, 1891a. Catalogue of fossil birds. Brit. Mus. (N.H.).

————, 1891b. On British fossil birds. *Ibis* Ser. 6, 3: 394-5.

MARPLES, B. J., 1946. Notes on some neogathous bird bones from the early Tertiary of New Zealand. *Trans. R. Soc. N.Z.* 76(2): 132-134.

MARSHALL, J. (Ed.), 1960. Biology and comparative physiology of birds. 2 vols. 8 vo. New York and London.

MILLER, L., 1935. New bird horizons in California. *Univ. Calif. Publ. biol. Sci.* 1: 79.

————, 1962. A new albatross from the Miocene of California. *Condor* 64: 471-2.

MURPHY, R. C., 1936. Oceanic birds of South America. 2 vols. 4 vo., *Amer. Mus. Nat. Hist.* New York.

PETERS, J. L., 1931. Check-list of birds of the world I. 8 vo. Cambridge, Mass., U.S.A.

PYCRAFT, W. P., 1899. On the osteology of the Tubinares. *Proc. zool. Soc. Lond.* for 1899: 381-411.

ROTHSCHILD, W., 1893. Description of new species of albatross in report of meeting for 17th May, 1893. *Bull. Br. Orn. Club.* 1(48): 58-9.

SALVIN, O., 1883. A list of the birds collected by Captain A. H. Markham on the west coast of America. *Proc. zool. Soc. Lond.* for 1883: 430.

————, 1896. Catalogue of Birds. Brit. Mus. (N.H.) 25: 440-454.

SEEBOHM, J., 1890. The birds of the Japanese Empire. 4 vo., London.

SIMPSON, G. G., 1965. A new fossil penguin from Australia. *Proc. Roy. Soc. Vict.* 79: 91-93.

SINGLETON, F. A., 1941. The Tertiary geology of Australia. *Proc. Roy. Soc. Vict.* 53: 1-126.

STIRTON, R. A., WOODBURNE, M. O., and PLANE, M. D., 1967. A phylogeny of Diprotodontidae and its significance in correlation. *Bur. Min. Resour. Aust. Bull.* 85: 149-160.

WETMORE, A., 1943. *Proc. New Engl. zool. Club.* 22: 66-67. (Not seen.)

————, 1956. A check list of the fossil and prehistoric birds of North America and the West Indies. *Smithson. misc. Collns.* 131 (5), Publ. 428.

Explanation of Plates

All figures approx. nat. size

PLATE 3

Lateral views of fossil and its living relatives

Fig. 1—*Diomedea chlororhynchos* Gmelin, B704, figured specimen, living, Queenscliff, Vict.

Fig. 2—*Diomedea thyridata* sp. nov., P24172, holotype partial bill, Black Rock Sandstone, U. Miocene, Beaumaris, Vict., G.B. Pritchard Colln.

Fig. 3—*Diomedea melanophris* Temminck, B9678, figured specimen, living, Portland, Vict.

PLATE 4

Ventral and dorsal views of the specimens in Plate 1

Figs. 1-3—Ventral views of B704, P24172 and B9678 respectively.

Figs. 4-6—Dorsal views of ditto.